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Myrmecotypus mazaxoides sp. nov. – a new ground-dwelling, carpenter ant-resembling sac spider species from the Bolivian orocline, with indirect evidence for species-specific mimicry (Araneae, Corinnidae, Castianeirinae)

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Abstract

A new ant-resembling spider species of the subfamily Castianeirinae, *Myrmecotypus mazaxoides* **sp. nov.**, from the Sub-Andean area of the Bolivian orocline is described. Adults of *M. mazaxoides* **sp. nov.** resemble the carpenter ant *Camponotus* cf. *melanoticus* Emery, 1894 and were observed on the ground of savanna-like habitats close to the entrances of formicaries of this ant. This study is the first to report a ground-dwelling species of *Myrmecotypus* O. Pickard-Cambridge, 1894; all the other species are arboreal.

Key Words

Arachnid, Bolivia, *Camponotus*, myrmecomorph, South America

Introduction

The Neotropical Castianeirinae genus *Myrmecotypus* O. Pickard-Cambridge, 1894 is a group of slender, fast-running spiders and currently includes 13 species (World Spider Catalog 2021). Six species are reported from South America, of which five have been recorded from Bolivia: *Myrmecotypus haddadi* Perger & Rubio, 2021, *M. iguazu* Rubio & Arbino, 2009, *M. niger* Chickering, 1937, *M. rubrofemoratus* Perger & Rubio, 2021, and *M. tahyinandu* Perger & Rubio, 2020 (World Spider Catalog 2021).

Potential ant models have been proposed for six of the known 13 species of *Myrmecotypus* (Perger and Rubio 2020a, 2021a). Morphologically, these forms resemble specific models of the ant tribes Camponotini and Dolichoderini. Models and mimics share a moderately elongated, truncate forebody, short petiole and sub-globose abdomen, and were predominately observed in arboreal habitats (Perger and Rubio 2020a). Ground-dwelling Neotropical Castianeirinae species have only been reported from the genera *Castianeira* Keyserling, 1879 (Reiskind 1969, 1977) and *Mazax* O. P.-Cambridge, 1898 (Reiskind 1977; Rubio and Danişman 2014). In the present contribution, an unknown, ground-dwelling species of *Myrmecotypus* from the Bolivian orocline is described, and indirect evidence for specific ant mimicry is presented.

Material and methods

Spiders and ants were collected manually from the ground and herbaceous vegetation. Photographs of live spiders and ants and their habitats were taken with a Panasonic Lumix GX-80 system camera fitted with a Panasonic H-HS3030 macro lens. Color and distribution of setae were described from photos of live specimens. Spiders were euthanized with ethyl acetate and stored in 70% ethanol. Preserved specimens were examined in 70% ethanol under a Nikon

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SMZ-U dissection microscope and identified using original and re-descriptions and keys (e.g., Rubio and Arbino 2009; Leister and Miller 2014; Perger and Rubio 2021b). A Nikon Coolpix 950 digital camera attached to the microscope was used to photograph all the structures to be illustrated. The digital photos were used as a template to draw the structures. Female genitalia were excised using a sharp entomological needle placed on a slide in lactic acid and observed under an AmScope XSG Series T-500 compound microscope. All measurements are expressed in millimeters and were taken using a micrometric ruler on the microscope. Photos were taken with a BK Plus Lab System by Dun, Inc. with a Canon 5DS Macro camera and a Canon 65 mm lens.

The descriptions refer to adult specimens. Morphological terms and description formats follow the recent studies on Castianeirinae spiders (Rubio and Arbino 2009; Leister and Miller 2014; Perger and Rubio 2020a, 2021b). Body length (BL) measurement refers to the distance from the anterior margin of the carapace to the posterior margin of the opisthosoma. The cephalic width was measured at the level of the posterior eye row when viewed dorsally. The length of the dorsal and epigastric sclerite was measured without the petiole, which is separated from the former both sclerites by a slight groove.

The following indices (*sensu* Reiskind 1969) were calculated: a) carapace index = carapace width / carapace length × 100; b) cephalic index = cephalic width / carapace width × 100; c) sternum index = sternum width / sternum length × 100; d) abdomen index = abdomen width / abdomen length × 100.

The following abbreviations are used in the text: AER, anterior eye row; AME, anterior median eyes; ALE, anterior lateral eyes; PER, posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes.

Arachnological collections are abbreviated as follows (curators in parenthesis):

CBF Colección Boliviana de Fauna, La Paz, Bolivia (R. Perger);

ZMH Zoological Museum Hamburg, University of Hamburg, Germany (D. Harms).

Ecoregion distribution

The ecoregion affinities of the species were investigated by visualizing the coordinates and a shape file of the regionalization of Bolivian ecosystems by Navarro and Ferreira (2011), by using the geographic information system QGIS (version 2.14.3, http://www.qgis.org/en/site/). Geographic coordinates are shown in decimal degrees with reference datum WGS84, and elevation in meters above sea level (m. a.s.l.).

Ant mimicry

In this study, an indirect, correlative method is employed to support mimicry, without studying the impact of receiver responses on mimic fitness. While correlations do not imply causality, correlative approaches are useful for investigating putative cases of resemblance between taxa and extrapolating the consequences of mimicry beyond a single, well-studied population (De Jager and Anderson 2019; Perger and Rubio 2020a, b, 2021a). To illustrate adaptive divergence between mimetic and non-mimetic phenotypes, we identified derived traits in the mimic that likely evolved in association with species-specific models and receivers.

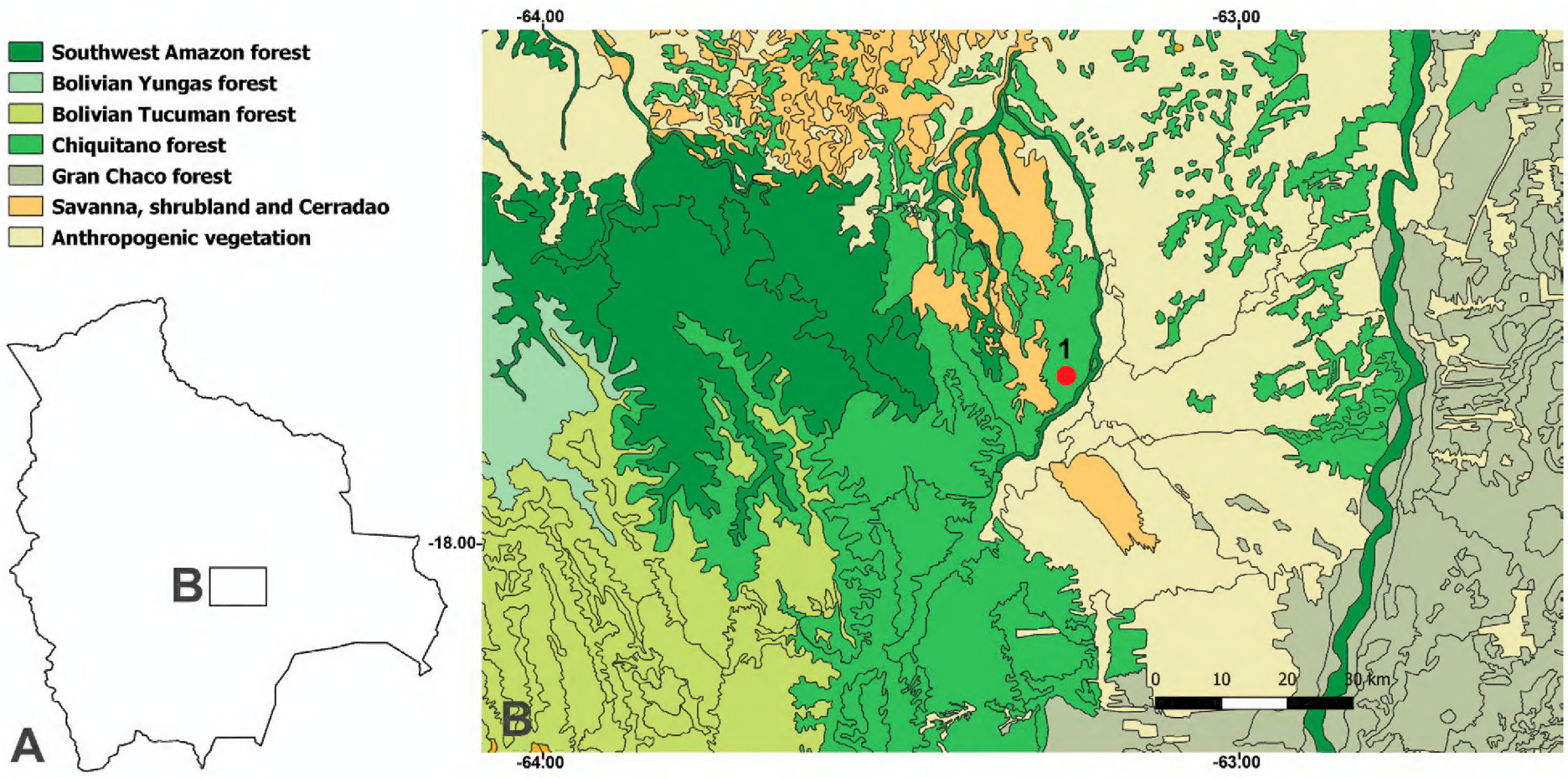

Figure 1. Ecoregion distribution of *Myrmecotypus mazaxoides* sp. nov., according to the regionalization by Navarro and Ferreira (2011); **A.** Bolivia; **B.** Sub-Andean area at the Bolivian orocline **1.** Collection locality of *M. mazaxoides* sp. nov., Santa Cruz de la Colina, Santa Cruz department; map produced with QGIS (version 2.14.3, http://www.qgis.org/en/site).

For the analysis of ant resemblance, we considered all ants that were collected in the surveyed location and were about the same body length as the spiders. The similarity was analyzed, based on a qualitative, descriptive assessment of integument color, shine, structure (e.g., appressed, erected, short, long) and color of setae and shape of body parts (e.g., abdomen shape: fusiform or ovate; apically pointed or rounded).

Taxonomy

Family Corinnidae Karsch, 1880
Subfamily Castianeirinae Reiskind, 1969

Genus *Myrmecotypus* O. Pickard-Cambridge, 1894

Type species. *Myrmecotypus fuliginosus* O. Pickard-Cambridge, 1894 (by original designation)

Diagnosis. Cephalic region wide (cephalic index range 64–89), carapace narrowed (carapace index < 60), without thoracic groove but with slight depression instead; PER wider than AER and almost straight to moderately recurved, AME larger than ALE, PME–PME greater than PME–PLE, PLE situated close to lateral margin of cephalic area; abdomen only very slightly petiolated; tibia I ventral spines paired in 2–2, 3–2, 3–3 or 4–4 arrangement; trochanter IV notch usually absent, with only a tiny one, if present (Perger and Rubio 2021b).

Myrmecotypus mazaxoides sp. nov.

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Figs 2–6, 7A, B

Type material. Holotype ♂ and ♀ allotype; BOLIVIA: Santa Cruz department, Santa Cruz de la Colina, Urubo; 17.760833°S, 63.24°W, 432 m. a.s.l., 21–28 Dec. 2019, R. Perger leg.; Cerrado-like grassland in urbanization (ZMH-A0014700-14701). Paratypes: 2 ♂, 5 ♀, same data as for preceding (ZMH-A0014707) • 6 ♂, 10 ♀, same data as for preceding; CBF.

Diagnosis. Amongst species of *Myrmecotypus*, an elongated and constricted abdomen is only found in *M. mazaxoides* sp. nov. (Figs 2, 3, 5) and *M. lineatus* (Emerton, 1909), the latter occurring along the east coast of the United States (Reiskind 1969). Additionally, both species share a broad carapace (carapace index ~47–52) and all eyes small and sub-equal (male of *M. lineatus* not described).

Females of *M. mazaxoides* sp. nov. can be distinguished from those of *M. lineatus* by the following characteristics: dorsum dark brown with an anthracite-greyish appearance in live condition (Fig. 7A, B) (in *M. lineatus*, carapace yellow-orange, dorsal sclerite of abdomen yellow, posterior part of abdomen dark purple-brown with light spots), coxae II-IV translucent white, I reddish (Figs 3B, 5) (in *M. lineatus*, all coxae light), dorsal sclerite pyriform (elliptic in *M. lineatus*), tibia I with 3 promarginal and 2 retromargial spines (tibia I spination 2–2 in *M. lineatus*); chelicerae with two promarginal teeth with distal tooth reduced to small denticle (3 promarginal teeth in *M. lineatus*); copulatory openings of epigyne anterior to spermathecae (lateral in *M. lineatus*).

Remarks. Reiskind (1969) noted the distinctness of *M. lineatus* while transferring this species from *Castianeira* to *Myrmecotypus*. The general habitus of *M. mazaxoides* sp. nov. resembles that of species of *Mazax* and possibly of some *Apochinomma* spp. Given that the generic taxonomy of Castianeirinae remains uncertain and requires detailed phylogenetic work (Perger and Rubio 2020a), we follow Reiskind (1969) and include the newly described species tentatively in *Myrmecotypus*. The generic taxonomy and morphological affinities to species of other genera of Castianeirinae are addressed in the discussion.

Description of male holotype. Body length 4.69; carapace length 2.17, width 1.11, carapace index 51; cephalic width 0.72, cephalic index 65; sternum length 0.93, width 0.67, sternum index 72; abdomen length 2.42, maximum width anterior part 0.76, maximum width posterior part 1.04, abdominal index 43; petiole length 0.10, width 0.29; dorsal sclerite length 2.32 (width agrees with abdominal width); epigastric sclerite length 0.62, width 0.74; ventral sclerite length 0.95, width 0.51; inframamillary sclerite length 0.09, width 0.15. AER 0.47; AME-AME 0.08; AME-ALE 0.02; PER 0.60; PME-PME 0.14; PME-PLE 0.11.

Carapace (Fig. 2A). Long pyriform, truncated anteriorly, front slightly convex, cephalic area laterally somewhat narrowed, carapace widest in middle, three slight concavities in posterior half, posterior margin straight. Dorsum weakly shiny, smooth, microsculpture reticulate with evenly distributed, fine pits, dark brown; short, appressed, separate, white and brassy setae, simple on cephalic area and feathery on thoracic area (setae providing an anthracite-greyish appearance in live condition), several relatively long, forward-pointing, dark setae on front of cephalic area.

Eyes. Eight sub-equal eyes formed in two rows; PER distinctly recurved; AER slightly recurved.

Chelicerae. Orange-brown, shiny, with separated erect dark setae, area between retro- and promarginal rows of cheliceral teeth orange-white with dense white setae, two retromarginal teeth and two promarginal teeth, with distal tooth reduced to small denticle.

Abdomen (Figs 2A, 3A). Elongated, distinctly constricted medially, posterior part broader than anterior part; petiole only moderately developed, very narrow medially, proximal margin strongly concave; dorsal sclerite almost completely covering abdomen dorsally and laterally; ventral sclerite not reaching to level of inframamillary sclerite, latter narrow, subrectangular, broader than long. Dorsum weakly shiny, smooth, microsculpture reticulate with evenly distributed, fine pits, dark brown; covered with separate, simple, short, brassy setae, abdominal setae long, simple, not sclerotized, second pair longer than first; in constriction, distinct band of relatively long, dense feathery white setae, on anterior part of abdomen

Figure 2. *Myrmecotypus mazaxoides* sp. nov., holotype male (**ZMH-A0014700**): **A.** Dorsal; **B.** Ventral. Scale bars: 0.5 mm. Please note that most setae are broken off due to storage in ethanol.

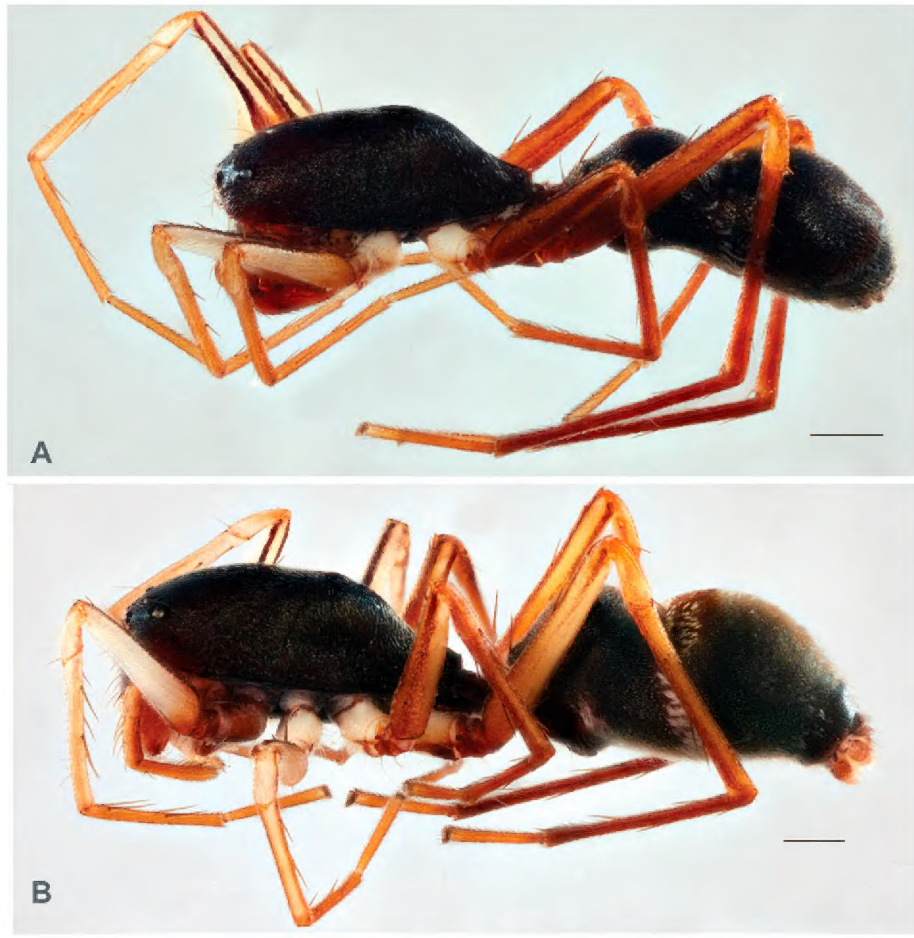

Figure 3. Lateral views of *Myrmecotypus mazaxoides* sp. nov.: **A.** Holotype male (**ZMH-A0014700**); **B.** Female allotype (**ZMH-A0014701**). Scale bars: 0.5 mm. Please note that most setae are broken off due to storage in ethanol.

similar band, less dense in the middle, on posterior part three to four indistinct bands of similar setae.

Legs. Coxae II and III translucent white, trochanters II and III dark yellow; coxae and trochanters I and IV reddish-brown; legs mostly sparsely covered with fine, golden setae, including feathery setae, dense in some areas, femora and tibia with separated, erect, long setae; femora I and II proximal fifths reddish, distal four-fifths laterally translucent, white and dark stripes along dorsal edges, remainder of legs I and II reddish-yellow; tibia I promarginal with 3 spines, retromarginal with 2 spines; femora and tibiae III and IV reddish-brown, dark grey stripes along dorsal sides; remainder of leg III orange-light brown; leg IV tarsus yellow; legs III and IV lined with short, appressed white feathery setae.

Palp. Pedipalp tibia with two distinct, long setae and several shorter setae (Fig. 4A, B), retrodistal margin with one small, obtuse tooth-like apophysis (Fig. 4D, E); maximum width of tibia 96% of maximum width of bulb when viewed retrolaterally; narrow genital bulb drawn out into long neck, with long, thin, sclerotized embolus with three coils and a basal ridge (Fig. 4C); sperm ducts with two loops, both lateral and basal to embolus tube (Fig. 4A, B).

Female allotype. Body length 6.23; carapace length 2.85; width 1.35; carapace index 47; cephalic width 1.00; cephalic index 74; sternum length 1.19; width 0.80; sternum index 67. Abdomen length 3.15; maximum width anterior part 1.24; maximum width posterior part 1.45; abdominal index 46; petiole length 0.16; width 0.45; dorsal sclerite length 1.04; width 0.88; epigastric sclerite length 0.74; width 0.92; inframamillary sclerite length 0.16; width 0.35. AER 0.59; AME-AME 0.10; AME-ALE 0.03. PER 0.80; PME-PME 0.18; PME-PLE 0.13.

Lateral constriction of abdomen indistinct (Fig. 5A), length of dorsal and epigastric sclerite one-third of abdominal length, dorsal sclerite pyriform, laterally not completely covering abdomen, ventral sclerite absent; coxa II–IV translucent yellow-whitish. Remaining somatic characters as in male.

Epigyne (Fig. 6). Epigynal plate forming part of the epigastric sclerite. Copulatory openings situated anterior to spermathecae, pointing in anterior direction. Copulatory duct running from anterior median part of spermathecae and connecting latter at posterior margin. Spermathecae oval, dorsally convex, wall more sclerotized laterally, fertilization ducts at postero-lateral margin.

Variation. Females (BL 6–6.5 mm) were larger than males (BL 4.8–5.2 mm). Sexual dimorphism in coxae color (coxae II-III translucent whitish in male, II–IV in female). The number of clearly distinguishable transversal bands of feathery setae on the abdomen varied between one or two in the median constriction and three or four closely before the apex. While the abdominal constriction of the male is determined by the shape of the large dorsal sclerite, it varied in females according to the nutritional or reproductive state and could be similarly constricted as in males.

Etymology. The specific epithet, *mazaxoides*, is derived from the Castianeirinae genus "*Mazax*" and "*oeidēs*" (Greek) = resembling or looking like and refers to the general resemblance of the habitus of this species to species of *Mazax*.

Geographical and ecological distribution. This species is only known from the type locality in the recently established urbanization of Santa Cruz de la Colina, Urubo, Santa Cruz department. This urbanization included empty plots with savanna grasslands, plant successions and bushes or houses with gardens. According to the ecoregion delineation by Navarro and Ferreira (2011), the forest in this area is considered Chiquitano forest. The urbanization was surrounded by a mosaic of forest fragments, Cerrado-like grassland and savanna. *Myrmecotypus mazaxoides* sp. nov. was observed foraging on the ground of open grassland during the day, under or between dense ground vegetation (Fig. 7A). Because of its

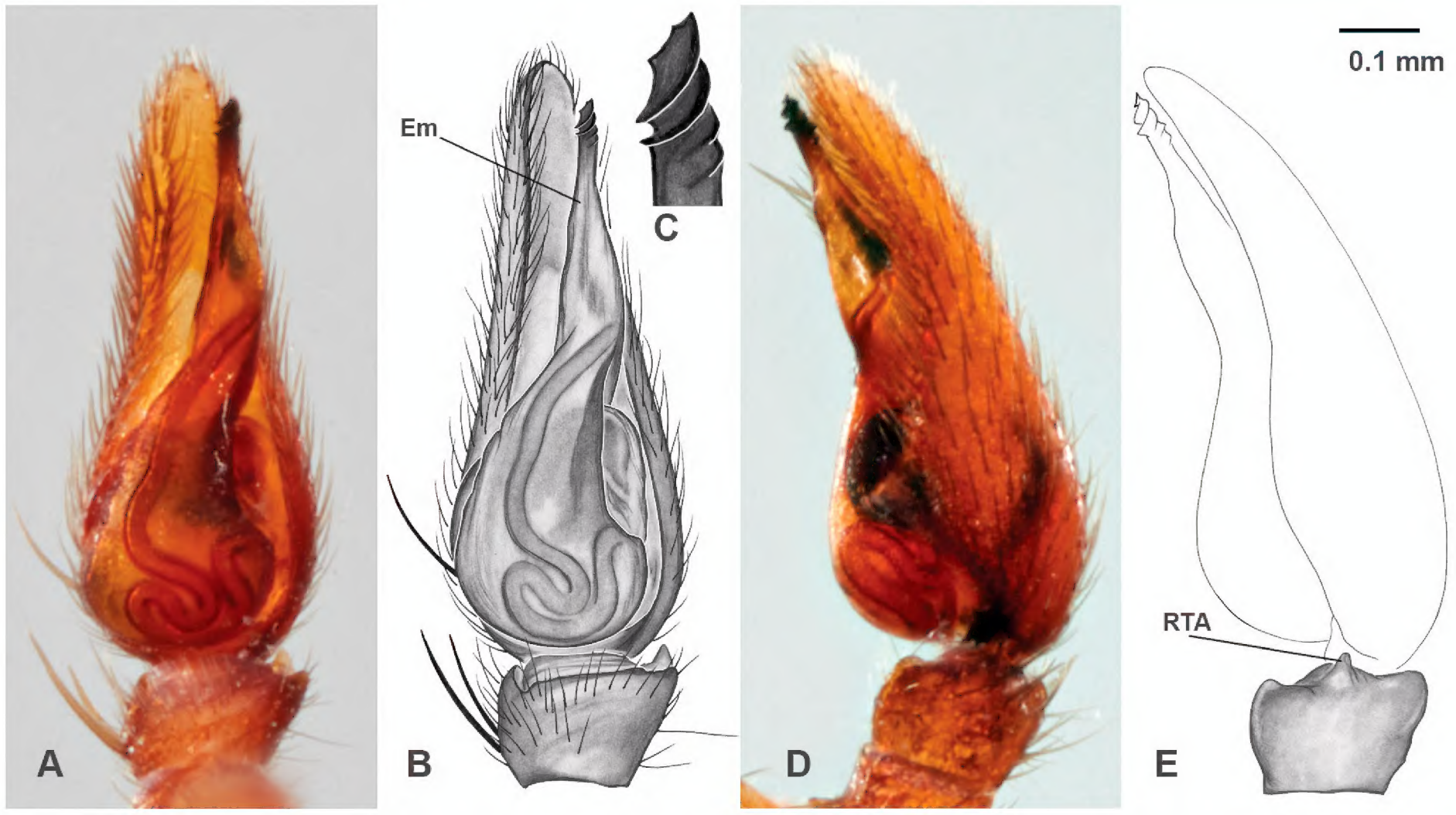

Figure 4. *Myrmecotypus mazaxoides* sp. nov., palp male holotype (**ZMH-A0014700**), **A, B.** Ventral view; **C.** Tip embolus; **D, E.** Lateral view. (Em = embolus; RTA = retrolateral tibial apophysis).

Figure 5. *Myrmecotypus mazaxoides* sp. nov., allotype female (**ZMH-A0014701**): **A.** Dorsal; **B.** Ventral. Scale bars: 0.5 mm. Please note that most setae are broken off due to storage in ethanol.

presence in open habitats, it is likely that the species also occurs in similar habitats in the Gran Chaco area in southern Bolivia, Paraguay and northern Argentina. Despite high sampling effort in several Bolivian forest ecoregions (Perger and Perger 2017; Perger and Rubio 2018, 2020a, b), the new species was not observed in forest habitats.

Myrmecotypus mazaxoides sp. nov. co-occurred with four different species of *Castianeira* (not determined) in the same habitat, three of which were commonly observed and had a dark body (blackish or black with grey) and red legs. A single male of *Mazax* cf. *ramirezi* Rubio & Danişman, 2014, was collected as well, among individuals of *M. mazaxoides* sp. nov.

Ant mimicry. Eleven ant species with a similar or larger body length than adults of *M. mazaxoides* sp. nov. (BL 4.8–6.5 mm) were found in the investigated plots. However, all individuals of the new species were collect-

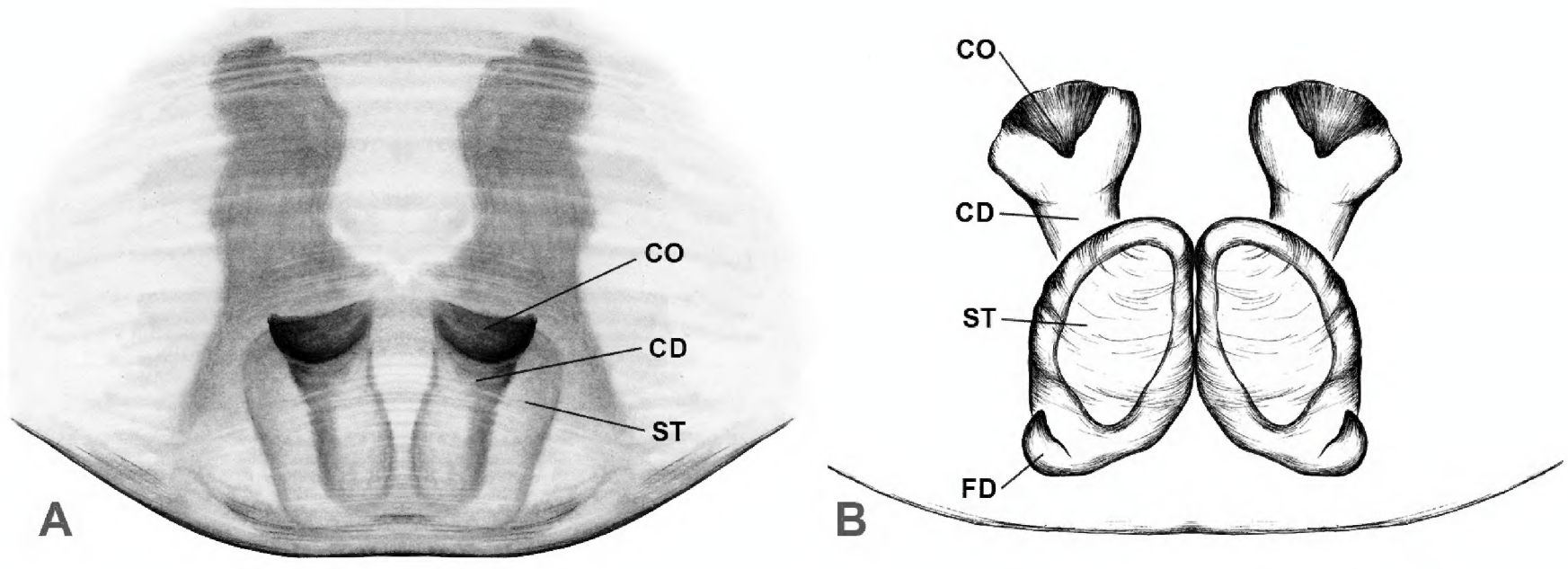

Figure 6. *Myrmecotypus mazaxoides* sp. nov., epigyne female allotype (**ZMH-A0014701**), **A.** Ventral view; **B.** Internal genitalia cleared, dorsal view. (CO = copulatory opening; CD = copulatory duct; ST = spermatheca; FD = fertilization duct).

Figure 7. Life habitus and morphological resemblance between spider and possible ant model: *Myrmecotypus mazaxoides* sp. nov., males: **A.** In natural habitat; **B.** On white background. *Camponotus* cf. *melanoticus* Emery, 1894 (minor workers): **C.** In natural habitat; **D.** On white background.

ed close to the entrance of subterranean formicaries of *Camponotus* cf. *melanoticus* Emery, 1894. *Myrmecotypus mazaxoides* sp. nov. and *C.* cf. *melanoticus* shared an elongated, sub-oval abdomen, a weakly shiny, dark brown integument with anthracite tinge, fine brassy pubescence and sparse white setae on the posterior abdomen, and completely red legs (Fig. 7). The reddish pedipalps of the spider resembled the reddish mandibles of the ants. Major workers of *C.* cf. *melanoticus* were unlikely models, as they were larger and had proportionally larger heads. The body length of adults of *M. mazaxoides* sp. nov. (BL 4.8–6.5 mm) was similar to the range of minor workers (BL 5.8–6.2 mm) of *C.* cf. *melanoticus.*

No other ant species with a weakly shiny, greyish body, short brassy pubescence or completely red legs was observed in the studied area. Two additional ant species had an oval abdomen, but one of those species had a brown pronotum and a black, shiny abdomen (*Camponotus* cf. *fastigatus* Roger, 1863), and the other species a reddish forebody and abdomen with golden pubescence (*Camponotus* cf. *blandus* Smith, F., 1858).

When the first author approached the individuals of *M. mazaxoides* sp. nov., they were hiding under ground vegetation (e.g., Fig. 7A). In contrast, individuals of *C.* cf. *melanoticus* started to run fast and erratically after coming into contact with the hand of the main author, and many approached and some successfully administered a bite. The ants also behaved aggressively towards individuals of *M. mazaxoides* sp. nov. that came to close to the entrance of the formicaries, attacking and biting the spiders. The spiders rapidly retreated after such agonistic behavior.

For about six months, the colony of *C.* cf. *melanoticus* was expelled by a colony of the larger *Camponotus renggeri* Emery, 1894, which was attracted by mealybugs on a nearby stand of introduced *Croton* plants. During the absence of *C.* cf. *melanoticus*, no individuals of *M. mazaxoides* sp. nov. were observed, despite a similar sampling effort. After the removal of the mealybugs by the main author, *C. renggeri* stayed away and the site was re-colonized by *C.* cf. *melanoticus* and *M. mazaxoides* sp. nov., indicating a strong mimetic relationship between these ants and spiders.

Discussion

Possible intergeneric relationships

Rubio and Arbino (2009) referred to the resemblance between *Myrmecotypus* and *Apochinomma*. While the Afrotropical species of *Apochinomma* have been revised by Haddad (2013), the generic placement of the Neotropical congeners remains uncertain. Rubio and Arbino (2009) questioned whether *Apochinomma* is present in the Neotropical region, suggesting that some Neotropical species of this genus may belong to *Myrmecotypus*. From the Neotropics, nine species of *Apochinomma* have been described, eight from Brazil and one from Guyana (World Spider Catalog 2021). *Apochinomma acanthaspis* Simon, 1896 (BL female type 5 mm), *A. armatum* Mello-Leitão, 1922 (BL female type 5 mm), *A. constrictum* Simon, 1896 (BL female type 5.2 mm) and *A. pyriforme* (Keyserling, 1891) (BL female type 6.7 mm) have an elongated, constricted abdomen. However, *A. acanthaspis* and *A. armatum* have the second pair of setae on the dorsal abdominal sclerite sclerotized to spines, indicating that both may belong to *Mazax* (Perger and Rubio 2020a). *Apochinomma constrictum* has all coxae red-brown and lacks transverse bands of setae and *A. pyriforme* can be distinguished by the AME larger than the other eyes, the PER straight, and comparably narrow (typical arrangement for *Castianeira*), and the femora II-IV yellow (see Keyserling 1891).

Generic placement

Because of the elongated, constricted abdomen, the general habitus of *M. mazaxoides* sp. nov. resembles that of *Mazax* species. *Myrmecotypus* and *Mazax* share a moderate to extremely weak thoracic groove and the AER straight to (moderately) recurved. Additionally, there is an overlap of the number of the tibia I ventral spines (*Myrmecotypus*: 2–2, 3–2, 3–3 or 4–4; *Mazax*: 3–3, 4-4, 5–5, or 6–6).

Both genera differ concerning their cephalic index (in *Mazax* the thoracic part is wider, resulting in a cephalic index of 53–64; in *Myrmecotypus* 64–92). In *Mazax* the AME are smaller than the ALE (larger in *Myrmecotypus*) and the abdomen has a distinct, rugose abdominal petiole (only slightly petiolated in *Myrmecotypus*). Additionally, except for both sexes of *M. ajax* Reiskind, 1969, males (and some females) of all known species of *Mazax* have the second pair of abdominal setae heavily sclerotized into spines.

In *M. mazaxoides* sp. nov., the subequal size of the eyes, the 3–2 ventral spination of tibia I and the elongated, constricted abdomen suggest that *M. mazaxoides* sp. nov. represents a transitional form between *Mazax* and *Myrmecoptypus*. However, because of the cephalic index (♂65; ♀74), the moderately developed petiole, and the simple abdominal setae, we tentatively place *M. mazaxoides* sp. nov. in *Myrmecotypus*.

Considering the uncertain relationships between *Myrmecotypus* and Neotropical *Apochinomma* and the possibility that *Myrmecotypus* is a polyphyletic group (Reiskind 1969), a proper phylogenetic analysis, including the analysis of DNA, is needed to facilitate a robust assessment of the generic relationships.

Mimicry

Based on co-occurrence patterns and morphological similarities, such as a moderately elongated, truncate forebody, short petiole, and sub-globose abdomen, Perger and Rubio (2020a) hypothesized that *Myrmecotypus* species are mimics of specific species of the ant tribes Camponotini or Dolichoderini. However, the six *Myrmecotypus* species for which ant models have been proposed and their putative models were predominately observed in arboreal habitats (Perger and Rubio 2020a, 2021a).

The morphological resemblance of *M. mazaxoides* sp. nov. to *Myrmecotypus* and *Mazax*, the latter being an exclusively ground-dwelling genus, and the occurrence of *M. mazaxoides* sp. nov. in ground habitats suggests that this species represents a transitional form between ground-dwelling and arboreal Castianeirinae lifestyles. A phylogenetic analysis may not only shed light on the generic relationships of Castianeirinae but also on the evolutionary history of ant mimicry in this subfamily.

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